

## A NEW LARGE MADTSOIID SNAKE FROM THE MIOCENE OF THE NORTHERN TERRITORY.

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### ABSTRACT

Eighteen large snake vertebrae from a single locality within the Camfield Beds (middle Miocene) at Bullock Creek, Northern Territory, Australia, represent a single individual of *Yurlunggur camfieldensis* new genus and species. The family Madtsoiidae is correctly referred to the Alethinophidia, but distinguished from all other Alethinophidian taxa by combinations of vertebral and cranial characters most fully represented in *Wonambi naracoortensis*.

KEYWORDS: Serpentes, Alethinophidia, Madtsoiidae, *Yurlunggur camfieldensis*, Miocene, Northern Territory.

### INTRODUCTION

Apparently primitive snakes similar to the South American *Madtsioia bai* Simpson, 1933, have been described from Upper Cretaceous to Eocene deposits in Madagascar, South America and Africa (Andrews 1901, 1906, Simpson 1933, Hoffstetter 1961, Albino 1986). The subfamily Madtsoiinae was recognised as an assemblage of primitive boids by Hoffstetter (1961) and raised to family status by McDowell (1987). The group was defined on the basis of vertebral morphology (Hoffstetter 1961, and see below), as diagnostic cranial material had not been described. Fossil snake vertebrae possessing the same distinctive features shared by *Madtsioia* and *Gigantophis* are also known in Australia, from Quaternary and (now) Tertiary deposits. *Wonambi naracoortensis* Smith, 1976 is similar in vertebral morphology to *Madtsioia bai* (Barrie 1990), and is the only madtsoiid yet described from Australia. It was widespread but apparently uncommon in southern and eastern Australia during the Late Pleistocene (Molnar 1982, Barrie 1990, McNamara 1990). The Madtsoiidae is thus completely Gondwanan in known distribution, and has the longest known fossil record of any group of snakes.

A long Australian history for the madtsoiids is implied by the presence of *Wonambi naracoortensis* in the Pleistocene, but Tertiary specimens

have not been described previously. A representative is here reported from Bullock Creek, and remains are also known from the Riversleigh deposits (Oligo-Miocene; Scanlon 1988, Archer *et al.* 1989, Scanlon in prep.) and Murgon (Eocene; Godthelp *et al.* 1992, Scanlon in press.) in Queensland. Vertebrae from the Oligo-Miocene Etadunna Formation of South Australia have been identified as snake (Estes 1984) and could also be madtsoiid, but insufficient descriptions are available.

### MATERIALS AND METHODS

The Bullock Creek snake fossils were found and prepared by P. Murray, D. Megirian and K. Roth, scattered among the remains of other vertebrates in a large mass of arenaceous limestone at the "Blast Site" locality of probable middle Miocene age (Woodburne *et al.* 1985). A pythonid, *Morelia antiqua* Smith and Plane, 1985 (emended here from *Morelia antiquus* to agree in gender), has already been described from the Camfield Beds based on a well-preserved dentary. Pythonid vertebrae, presumably representing the same taxon, and an elapid vertebra have also been obtained and are under study. Earlier collections made at the Blast Site locality at Bullock Creek, now held at the Na-

tional Museum of Victoria, included large snake vertebrae which may belong to the same skeleton as the material described here (T.H. Rich, pers. comm.), but they have not yet been examined.

Eighteen madtsoiid vertebrae from this site have been studied, all apparently representing a single large individual described as *Yurlunggur canfieldensis* n. gen. and sp. Its vertebrae are distinguished from those of previously named genera by morphology of articulating surfaces, neural spine and hypapophysis, and the sample of separated vertebrae allows a description of aspects of intracolumnar variation in the precaudal region. Terminology for vertebrae follows Auffenberg (1963) and Hoffstetter and Gase (1969).

Comparisons are based on figures and descriptions in the literature, articulated skeletons of pythonids (*Morelia spilota*, *Liasis olivaceus*, *L. fuscus*, *L. stimsoni*, *Aspidites melanocephalus*, *Python molurus*; Queensland Museum, Australian Museum) and fossil material representing *Wonambi naracoortensis* (South Australian Museum, Australian Museum, and private collection of D.J. Barrie) and undescribed madtsoiid species from Riversleigh and Murgon, Queensland (Queensland Museum collections, under study in Sydney).

## SYSTEMATICS

### Order Squamata Oppel, 1811

### Suborder Serpentes Linnaeus, 1758

### Infraorder Alethinophidia Nopcsa, 1923

Snakes with anterior dentigerous process of palatine, and trigeminal foramen divided. These characters are unknown for most madtsoiids, but the palatine and prootic have been described in *Wonambi naracoortensis* (Barrie 1990), which possesses the apomorphic states of the Alethinophidia.

### Family Madtsoiidae Hoffstetter, 1961

**Diagnosis.** (Modified from Hoffstetter 1961; vertebral features only). Accessory (prezygapophyseal) processes absent; zygapophyses strongly inclined above horizontal; width across paradiapophyses nearly as great or greater than width across prezygapophyses; paracotylar foramina present on most vertebrae; parazygantral foramina present on most vertebrae; neural spine usually step-like in profile, narrow anteriorly, thicker and higher posteriorly.

### *Yurlunggur* n. gen.

**Type species.** *Yurlunggur canfieldensis* n. sp.

**Diagnosis.** Large snakes (estimated to exceed 5m in length) differing from other madtsoiid genera in the following combination of vertebral characters: neural spine low but posteriorly overhanging zygantrum; zygapophyses inclined at less than 22° from horizontal, and approximately equal to diapophyses in width; condyle and cotyle moderately depressed and wider than high.

Comparable in size to species of *Madtsoia*, *Gigantophis* and *Wonambi*, and considerably larger than species of *Alamitophis*, *Patagoniophis* and *Rionegrophis*. Neural spine considerably lower and less steep than in species of *Wonambi*, *Madtsoia*, *Alamitophis* and *Rionegrophis*, but somewhat higher (at similar positions in the column) than in *Gigantophis garstini* and much more developed than in *Patagoniophis parvus*. Neural canal trifoliate in section, not triangular as in species of *Rionegrophis* and *Patagoniophis*, and somewhat wider than deep. Condyle and cotyle more oblique and depressed than in *Gigantophis garstini* and zygosphenes relatively higher and narrower. Postzygapophyses aligned more obliquely posteriorly than in species of *Madtsoia* and *Wonambi*, and less distinct in dorsal view from interzygapophyseal ridge (thus more similar to species of *Gigantophis* and the smaller Patagonian genera).

**Etymology.** *Yurlunggur* is the name of the mythic Rainbow Serpent in the language of the Ngolju (Dua and Jiritja) people of north-eastern Arnhem Land, Northern Territory (Mountford 1978). Gender is masculine.

### *Yurlunggur canfieldensis* n. sp.

**Type Locality.** 'Blast Site', Bullock Creek Local Fauna, Camfield Beds, north central Northern Territory.

**Age.** Middle Miocene, approx. 12 MYBP (Woodburne *et al.* 1985).

**Specific diagnosis.** As for the genus, until additional species are described.

**Material.** HOLOTYPE: A partial skeleton presently represented by 18 precaudal vertebrae and 11 rib fragments, separately registered in the Northern Territory Museum (NTM) vertebrate fossil collection. These are listed below in order from anterior to posterior, as interpreted here (number in brackets), giving the specimen numbers, and a brief description of the condition of the fossils:



- (1) P895-5, missing zygosphenes and right prezygapophysis;
- (2) P895-3, right anterior portion sheared off with damage to zygosphenes, cotyle and postzygapophyseal facet, prezygapophysis absent; hypapophysis broken below condyle;
- (3) P894-5, left parapophysis damaged, otherwise complete;
- (4) P87115-1, complete except for distal part of hypapophysis;
- (5) P8695-128, with damage to right parapophysis, posterior part of hypapophysis and neural arch, missing right postzygapophysis;
- (6) P8695-169, missing zygosphenes, left pre- and postzygapophyses, and postero-ventral part of centrum including condyle;
- (7) P87103-23, complete;
- (8) P8695-243, crack through left neural arch, slight damage to left prezygapophysis and diapophysis;
- (9) P8695-244, neural spine damaged, and with a single shear fracture extending from ventral midline to *margo lateralis* so that the left paradiapophysis is missing, and pre- and postzygapophyses, hypapophysis and cotylar rim are incomplete;
- (10) P8695-25, slight breakage to paradiapophyses and right prezygapophysis;
- (11) P8695-245, missing anterolateral corner of left prezygapophysis;
- (12) P8695-246, missing right prezygapophysis, paradiapophysis, part of zygosphenes and cotylar rim;
- (13) P8695-127, complete but cracked through right side of cotyle, paradiapophysis and neural arch, slightly distorted;
- (14) P87103-22, right side complete except for breakage to cotylar rim, left side mostly missing (zygosphenes and neural canal almost complete);
- (15) P8695-23, left side of zygosphenes broken, cotylar rim damaged, vertebra broken across horizontally and rejoined with slight distortion;
- (16) P87103-24, posterior part of neural spine and narrow section of zygantral roof missing;
- (17) P8692-28, postero-ventral part of centrum (from just behind cotyle) sheared away, particularly on right where postzygapophysis and part of paradiapophysis are also missing; crack through left side of neural arch with slight distortion;

(18) P8695-247, complete; neural canal remains filled with matrix.

No cranial or caudal remains have yet been obtained, but some partial ribs have been collected and are held at the NTM: 4 rib-heads (P87108-21, P8792-24, P8792-23, P8695-261) and 7 rib shafts (P8695-260, -262, -263, -264, P87108-17, -18-19 (fit together) and -20).

**Description.** *Body regions.* The 18 vertebrae are of three general types corresponding to anterior, middle and posterior regions of the trunk. Number 1 is from a position close behind the head (as indicated by the possession of processes on the posterior margin of the neural arch, which occur up to the seventh vertebra in the pythons examined), but vertebrae 1 to 10 (Fig. 1, A-C) form a relatively smooth series which increase in overall size while hypapophysis depth reduces, anterior to posterior, as in the anterior region of modern snakes. Number 10 is the largest vertebra in the sample, but larger elements may have occurred in the unrepresented mid-thoracic region. Also in this missing region, the transitions from single to double hypapophysis, and from flat to concave zygosphenes would have occurred. Vertebrae 11 to 17 (Fig. 1, D-E) have low hypapophyses which are double, lateral structures at the posterior end of a flattened haemal keel rather than a single median process. These vertebrae also have the zygosphenes and zygantrum strongly concave dorsally, a regional feature not seen to the same extent in other snakes. Number 18 (Fig. 1, F) is of similar size to no. 1. It is typical of posterior trunk vertebrae of snakes in being long and wide relative to depth and in having deep grooves separating the haemal keel and cotyle from the *margo ventralis* and parapophysis on each side. In the region represented by no. 18 the zygosphenes are once again relatively flat, not "curled up" as in 11-17, and the paired hypapophyses are located further from the condyle.

*Morphology.* The centrum is short and wide, in ventral view approximating an equilateral triangle truncated posteriorly (but relatively longer in no. 18). The cotyle is about as wide as the zygosphenes in anterior trunk and cloacal regions, but wider than the zygosphenes in the intermediate region. The condyle is moderately oblique. The underside of the centrum is slightly to strongly concave on either side of the haemal keel.

The hypapophysis of each anterior vertebra extends from a low ridge immediately below the cotyle, to a deep keel ending just anterior to the



Fig. 1. Vertebrae of holotype *Yurlunggur camfieldensis* in (top to bottom) lateral, anterior, posterior, dorsal and ventral views. A (1), P895-5; B (4), P87115-1; C (8), P8695-243. Scale bar equals 2 cm.



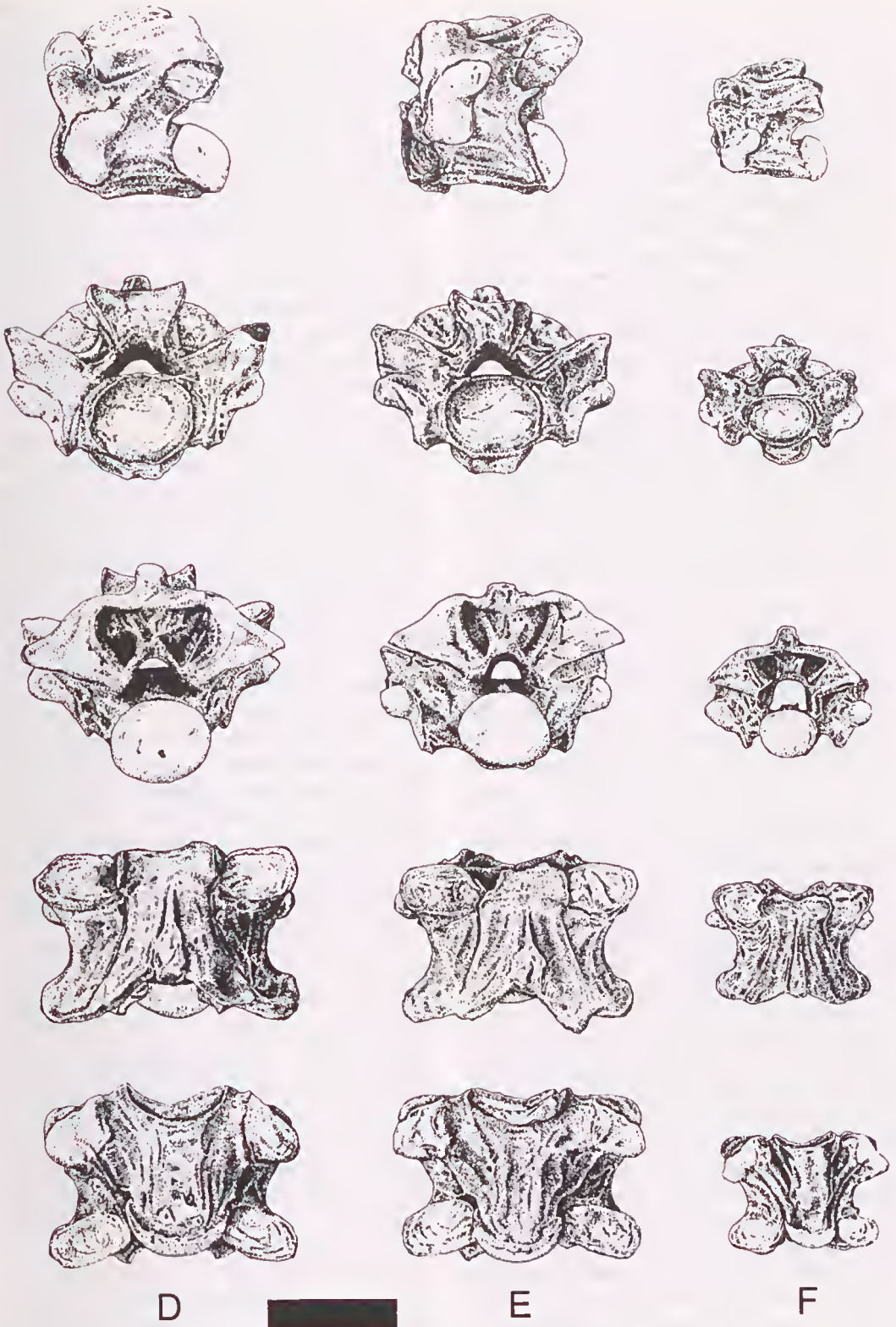


Fig. 1. (cont.): D (11), P8695-245; E (15), P8695-23; F (18), P8695-247. Scale bar equals 2 cm.

condyle. This keel is rounded in section anteriorly (approx. 2/5 of centrum length) and at the deepest, most posterior part (approx. last 1/5), while the middle part is more blade-like. In lateral view, the anterior part is concave ventrally, set off by a more or less distinct step-like inflexion from the straighter middle section (more or less strongly oblique, steepest in no. 4), while the posterior part of the ventral margin is convexly rounded and continuous with the near-vertical posterior edge below the condyle (more oblique in 1 and 2). Between anterior and posterior edges of the hypapophysis, the lines of inflexion between the lateral concavity and wedge-like keel form low but distinct longitudinal ridges.

The hypapophyses of more posterior vertebrae are represented by more extensive paired, low parallel ridges extending from the cotylar rim to just anterior to the condyle, defining a flattened, rectangular haemal keel which is somewhat concave ventrally in transverse and longitudinal section. The ridges end posteriorly in dorsoventrally compressed, diverging nipple-like processes extending below (but anterior to) the cotylar rim, some of which have a rough, pitted surface and/or conical tips free of the ventral face of the centrum. In the most posterior vertebra, possibly very close to the cloacal region, these processes are in a more anterior position (approx. 2/3 centrum length from cotylar rim). They face directly laterad, are elongated anteroposteriorly, and their surfaces are quite smooth.

The zygapophyses are inclined at 17–21° above the horizontal (steepest in no. 10–14), defining planes which intersect the neural canal near the middle of its height, corresponding to the position of the internal lateral ridges. The articular facets are roughly rectangular through most of the trunk. The long axes of prezygapophyses are nearly directly transverse, while those of postzygapophyses are more oblique (extending posterolaterad) and without the angular distinction from interzygapophyseal ridges seen in species of *Woumbi* and *Madisoia*. In no. 1 the zygapophyses are narrower, and hence their axes diverge less from the sagittal plane. The anterior edge of the prezygapophyseal facet is slightly concave on anterior vertebrae, becoming straight and then convex posteriorly. In no. 18, all facets are more rounded in outline. Growth rings are clearly visible on all articular facets excluding the condyle and paradiapophyses. Prezygapophyseal (accessory) processes are absent as such, but the surface of the prezygapophyseal buttress is convex and forms a low horizontal

ridge for muscle attachment parallel with, and extending slightly lateral to extremity of facet.

The zygosphenes are thick, mostly deeper than the neural canal (shallower in no. 1, about equal in no. 18), and its facets diverge at 30–34° from the vertical, defining planes which intersect at or below the floor of the neural canal. Zygosphenal facets are roughly semicircular in anterior vertebrae, having a straight leading edge which becomes convex posteriorly. The anterior face of the zygosphenes has a median concavity below, passing smoothly (or with vertical striations, but no transverse ridge) into the roof of the neural canal, between lateral ridges formed by the zygosphenal facets. The upper part of the anterior face is near vertical in most anterior vertebrae, and limited above by a strong transverse ridge, which is weaker at the midline forming a median concavity seen from above, as in species of *Madisoia*. More posteriorly (no. 11–17) this ridge lies below and behind the upper edge of the lateral facets so that the anterior and dorsal faces of the zygosphenes are strongly concave across the midline. The facets, which in anterior vertebrae are slightly concave laterad near their upper extremities, are in the posterior region strongly convex, and visible from above. In no. 18, the zygosphenes are of similar form to no. 3–10, though much less deep. Number 3 has the zygosphenes concave above, but not as strongly as in the posterior trunk, and the facets face ventrolaterad.

The neural arch and zygantrum closely follow the form of the zygosphenes in their variation along the column; the zygantral roof is of approximately uniform thickness across the width of each vertebra, its posterior edge facing somewhat dorsad medially but vertical or inclined slightly ventrad at the lateral extremities or "shoulders". In no. 1 there are distinct dorsolateral protuberances at these points, increasing leverage for short-span dorsal flexors which attach in this region; these are in a similar position to the 'pterapophyses' occurring in trunk vertebrae of the genera *Palaeophis* and *Pterosphenus* (Palaeophidae), but they seem more comparable to features of anterior neck vertebrae in pythons. Number 15 also has an asymmetric posterior extension from the same point, which is the only clear case of irregular bone growth in the sample.

The *margolateralis* is smoothly concave, without a sharp angle anterior to the postzygapophysis. The neural spine is low, composed of two portions: a narrow lamina anteriorly, rising from just anterior to the constriction behind the



zygosphene; and a higher columnar part posteriorly, sloping back to overhang the zygantrum, and bearing an irregular expansion (elliptical, triangular or roughly pear-shaped) of its dorsal surface for tendinous attachments. The dorsal edge of laminar portion varies from a nearly straight oblique edge (no. 2 and 4), through leveling off for a short section near its upper extremity (no. 10), to having only a short steep anterior section and much longer shallowly oblique 'step' (no. 11-18).

The paradiapophyses are similar in most respects to species of *Madtsoia* and *Wonambi*, varying somewhat in relative size and position along the column, but in this sample not greatly exceeding the zygapophyses in maximum width (in contrast to those genera).

Paracotylar and parazygantral foramina are present on all vertebrae, as well as subcentral, zygantral and several groups of lateral foramina. Paracotylar, ventrolateral (posterior to diapophysis), midlateral (posterior to zygosphene) and dorsolateral foramina (at base of neural spine, sometimes extending posterolaterally near edge of neural arch) occur as clusters of small apertures, mostly in distinct bowl-like depressions within larger concave areas, and numbering 2-5 (or more numerous where dorsolateral foramina occur over a larger area). Parazygantral and zygantral foramina are larger, and occur individually as deep pits directed anteroventrad and mediad from the posterior surface of the vertebra. There are frequently two or more pairs in each case, the more ventral being largest and most symmetrical in occurrence and position. A single pair of subcentral foramina is present, usually small but one member enlarged in a few cases, and in no. 9 both foramina are on the same side of the midline.

**Ribs.** The ribs of *Yurlunggur camfieldensis* are similar to those of *Wonambi naracoortensis* (see Barrie 1990) in shape of head and shaft, and presence of only small foramina in the dorsal groove. Both these forms differ from *Madtsoia bai* (Simpson 1933) in the virtual absence of an anterodorsal process adjacent to the head, and thus resemble more typical alethinophidians.

**Etymology.** The specific epithet refers to the type locality.

## DISCUSSION

The type specimen of *Yurlunggur camfieldensis*. The recognition of individuals is

a necessary step in the description of taxa, but may be problematic in the case of disarticulated material. The interpretation that the material described here represents a single individual is supported by two kinds of evidence. First, all the vertebrae and identifiable ribs are from a single quarry site and horizon, whereas madtsoiid remains are unknown from other sites in the area. Thus madtsoiids appear to be a rarely preserved element of the local fauna, and the likelihood of two or more skeletons being intermingled is correspondingly low. Second, vertebral measurements are interpreted as consistent with normal variation dependent on position within the column, where position is indicated by hypapophysis type and proportions (e.g. Hoffstetter & Gasc 1969). Neural canal height, in particular, varies little within the sample, while other linear dimensions differ considerably between mid-trunk and extreme vertebrae. Similar morphoclines are seen in skeletons of extant pythonids (unpublished data).

Estimates of the size of snakes based on vertebral dimensions can only be imprecise because, even if the relative position of the vertebrae within the column can be inferred accurately, the total number cannot be known unless the whole skeleton is found. Simpson (1933) was fortunate enough to have an articulated sequence of 40 vertebrae from which to describe *Madtsoia bai*, but admitted that his estimate of around ten metres could only be a rough guess because of the uncertain vertebra number. Other estimates of the size of madtsoiids have been based on comparison with pythons: Andrews (1901) derived a length estimate of approximately 30 feet (9m) for *Gigantophis garstui* by assuming an equal proportion between the width of the largest vertebra and total length, in the fossil species and a specimen of the modern *Python uolurus*. Barrie (1990) made measurements of vertebrae from two partial skeletons of *Wonambi naracoortensis*, and assuming a similar 'shape' (dependence of size and proportions on position in the column) to a modern python *Morelia spilota variegata*, used an analog technique to estimate a total vertebra number of 350 to 400, and arrived at length estimates for the larger *Wonambi* of 5.39 to 6.13m. The present specimen appears to have been considerably larger than the Henschke's Cave *Wonambi*, for the largest vertebrae are about the same size in each case, but the middle region of the body is unrepresented in the Bullock Creek material. It can therefore be suggested conservatively, assuming similar verte-

bral numbers in both madtsoiid genera, and similar body proportions to the python, that this specimen of *Yurlunggur camfieldensis* was greater than 5m in length.

**The classification of the Madtsoiidae.** The monophyly of the Madtsoiinae, and its systematic position within the Serpentes, have been subject to doubt in the absence of cranial remains. Their retention within Boidae by Hoffstetter (1961), Smith (1976) and Albino (1986), among others, was appropriate given the traditional palaeontological diagnoses in which Boidae was clearly paraphyletic or polyphyletic. Madtsoiid vertebrae possess a number of plesiomorphic character states for alethinophidian snakes. McDowell's (1987) classification of the Madtsoiidae within an explicitly paraphyletic group, the Chelophidia, reflects a view that madtsoiids were "more primitive than *Diuiylisia*", but the differences cited in support, such as shape and lateral projection of the paradiapophyses, position and slope of the zygapophyses, and absence of a prezygapophyseal process, are not as clear as was supposed (see Rage and Albino 1989).

When comparisons are made with *Diuiylisia patagonica* as an outgroup to the Alethinophidia (the vertebrae are described by Hecht 1982, and Rage and Albino 1989), the following plesiomorphic characters of the Madtsoiidae can be noted: paracotylar foramina are present (variable in *Diuiylisia*); zygapophyses are inclined well above the horizontal (but less so than in lizards or *Lapparentophis defrennei* Hoffstetter, 1959); the anterior edge of the zygosphenes is indented (lacking a median prominence or transverse ridge); the neural spine consists of a thin anterior lamina and posterior column; the hypapophysis is prominent on anterior vertebrae but reduced or absent in the middle and posterior trunk; the diapophyses are prominent laterally, and in posterior vertebrae they project beyond the prezygapophyses. Taken together, these plesiomorphic characters exclude the madtsoiids from membership of any extant families: indeed, reduction of diapophysis width could be seen as a synapomorphy of the Alethinophidia. However, there remains a considerable phenetic similarity between madtsoiids and some members of the Boidae, which includes forms with relatively plesiomorphic vertebrae and has therefore been very broadly defined in the palaeontological literature (e.g. Hoffstetter 1961).

Several vertebral characters can be regarded as synapomorphies defining the Madtsoiidae:

they possess large and distinct parazygantral foramina on all but rare vertebrae (exceptions noted in *Wonambi* by Smith 1976, and in *Madtsoia* by Albino 1986); posterior trunk vertebrae have laterally paired swellings of the flattened haemal keel, here referred to as paired hypapophyses, at least in *Madtsoia* (Simpson 1933), *Wonambi* (Smith 1976) and *Yurlunggur* n. gen.; and prezygapophyseal accessory processes are absent, though they may be represented by a low horizontal ridge ventral and slightly lateral to the facet. Of these, the madtsoiid condition is matched only by the absence of a prezygapophyseal process in some Boinae which, if the monophyly of Boidae is accepted, must be convergent.

Thus the Boidae (comprising Boinae and Erycinae, as in McDowell 1987) is difficult to separate clearly from the Madtsoiidae in terms of easily observed apomorphies of the vertebrae alone (Underwood 1976), although in practice madtsoiid vertebrae are readily identified. Analysis of isolated vertebrae seems unable to resolve the phylogeny of snakes at this level. Evidence from the skull must decide whether madtsoiids are derived among the Boinae (Underwood 1976), "more primitive than *Diuiylisia*" (McDowell 1987) or represent a distinct lineage close to the origin of the Alethinophidia.

Barrie (1990) describes cranial material of *Wonambi naracoortensis*, regarded as a probable relative of *Madtsoia* spp. (Smith 1976), and finds characters indicating a position within the Alethinophidia (presence of a palatine dentigerous process and divided trigeminal foramen) but distinct from pythons and boas, and plesiomorphically similar to acrochordids and, particularly, to tropidophcids (in palatine morphology, number and relative size of teeth, symmetrical vidian canals and a persistent cerebral foramen). This contrasts with both of the previous phylogenetic hypotheses, and is the basis for the classification adopted in this paper.

The multiplication of genera in the Madtsoiidae might be seen as undesirable, but in such a long-lived and geographically widespread lineage diversity is to be expected. It is useful at this stage to name fossil forms pending better resolution of systematics within the group. The alternative to erecting new genera is to lump together forms as different in vertebral morphology as distinct living families, or which lived on separate continents tens of millions of years apart; or to describe remains without naming them; or to fail to describe them altogether. A thorough



phylogenetic analysis of the included taxa will use evidence from the vertebrae (including intracolumnar variation), ribs, and from jaw and braincase elements, and the evolutionary polarities of characters may be determined from outgroup comparisons with Dinilysiidae and numerous families of alethinophidians. Such a rigorous phylogenetic analysis of the Madtsoiidae is beyond the scope of this paper.

Nevertheless, a number of dichotomies or morphoelines have been indicated in the diagnosis above which are potentially useful for such an analysis, such as: maximum known size, neural spine height and steepness, shape of neural canal (trifoliate except in *Rionegrophis* and *Patagoniophis*, where it is distinctly triangular - but this is possibly a feature of the anterior body region as suggested for palaeopheids by Rage 1983), angle of inclination of zygapophyses, width and depth of zygosphenes, width of diapophyses relative to prezygapophyses, shape and inclination of condyle, inclination of postzygapophyses from the transverse plane, and angulation of interzygapophyseal ridge (*margo lateralis*). *Madtsoia*, *Alamitophis*, *Rionegrophis* and *Wonambi* have a high neural spine, long axis of postzygapophyses transverse, and angulate *margo lateralis*. *Gigantophis* and *Yurlunggur*, in contrast, have a moderate neural spine, postzygapophyses inclined posteriad and *margo lateralis* smooth. *Patagoniophis parvus* is distinguished from other described forms by its very low neural spine, but a low spine is also seen in specimens from the Australian Eocene (Scanlon in press). Whether these groupings represent phylogenetic units, or adaptive complexes related to body form, locomotion or dietary specialisation, can not be determined until more evidence is available on phylogenetic relationships between at least some of the genera. It seems likely, by analogy with living forms, that the madtsoiids with low neural spines were terrestrial, while those with high neural spines may have had some combination of aquatic, arboreal and saxicoline habits.

Further remains of *Y. caufieldensis* are likely to be discovered in future, as the type locality continues to be worked by the NTM. In addition, material referable to *Yurlunggur*, *Wonambi* and possibly new madtsoiid taxa is known from Oligo-Miocene and Eocene deposits in Queensland, and will be described in forthcoming publications. Madtsoiids appear to have formed a major component of Australian snake faunas

throughout the Tertiary, the extent and pattern of whose radiation remains to be seen.

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## REFERENCES

- Albino, A.M. 1986. Nuevos Boidae Madtsoiinae en el Cretaceo tardio de Patagonia (Formacion Los Alamos, Rio Negro, Argentina). In Bonaparte, J.F. (ed.): *Simpósio Evolucion de los Vertebrados Mesozoicos. IV Congreso Argentino de Paleontología y Bioestratigrafía, Mendoza*: 15-21.
- Andrews, C.W. 1901. Preliminary notes on some recently discovered extinct vertebrates from Egypt (Part II). *Geological Magazine* 8: 434-444.
- Andrews, C.W. 1906. *A descriptive catalogue of the Tertiary Vertebrata of the Fayum, Egypt*. British Museum, London.
- Archer, M., Godthelp, H., Hand, S.J. and Megirian, D. 1989. Fossil mammals of Riversleigh, north-western Queensland: preliminary overview of biostratigraphy, correlation and environmental change. *Australian Zoologist* 25 (2): 29-65.
- Auffenberg, W. 1963. The fossil snakes of Florida. *Tulane studies in zoology* 10(3):131-216.
- Barrie, D.J. 1990. Skull elements and additional remains of the Pleistocene boid snake *Wonambi naracoortensis*. *Memoirs of the Queensland Museum* 28 (1): 139-151.
- Estes, R., 1984. Fish amphibians and reptiles from the Etadunna Formation, Miocene of South Australia. *Australian Zoologist* 21: 335-343.
- Godthelp, H., Archer, M., Cifelli, R., Hand, S.J. and Gilkeson, C.F. 1992. Earliest known Australian Tertiary mammal fauna. *Nature* 356:514-516.
- Hecht, M.K. 1982. The vertebral morphology of the Cretaceous snake, *Dinilysia patagonica* Wood-

- ward. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 1982 (9): 523-532.
- Hoffstetter, R. 1959. Un serpent terrestre dans le Crétacé inférieur du Sahara. *Bulletin de la Société Géologique de France* 7(1): 897-902.
- Hoffstetter, R. 1961. Nouveaux restes d'un serpent boidé (*Matsoia madagascariensis* nov. sp.) dans le Crétacé supérieure de Madagascar. *Bulletin du Muséum National d'Histoire Naturelle, Paris*. 33(2): 152-160.
- Hoffstetter, R. and Gasc, J.P. 1969. Vertebrae and ribs of modern reptiles. In Gans, C. (ed.) *Biology of the Reptilia. Vol. 1*. pp. 201-310. Academic Press, London.
- McDowell, S.B. 1987. Systematics. In Seigel, R.A., Collins, J.T.C. and Novak, S.S. (eds) *Snakes: Ecology and Evolutionary Biology*. pp. 1-50. MacMillan, New York.
- McNamara, G.C. 1990. The Wyandotte Local Fauna: a new, dated, Pleistocene vertebrate fauna from northern Queensland. *Memoirs of the Queensland Museum* 28 (1): 285-297.
- Molnar, R.E. 1982. Cenozoic fossil reptiles of Australia. In Rich, P.V. and Thompson, E.M. (eds) *The vertebrate record of Australia*. pp. 227-234. Monash University, Melbourne.
- Mountford, C.P. 1978. The Rainbow-serpent myths of Australia. In Buehler, I. and Maddock, K. (eds) *The Rainbow Serpent; a chromatic piece*. Mouton Publishers, The Hague/Paris: 23-98.
- Rage, J.-C. 1983. *Palaeopliis colossaeus* nov. sp. (le plus grand serpent connu?) de l'Eocène du Mali et le problème du genre chez les palaeopheinae. *Comptes Rendus de l'Académie des Sciences* 296, Ser. III: 1029-1032.
- Rage, J.-C. and Albino, A.M. 1989. *Dinilysia patagonica* (Reptilia, Serpentes): matériel vertébral additionnel du Crétacé supérieur d'Argentine. Etude complémentaire des vertèbres, variations intraspécifiques et intracolumnaires. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 1989(7): 433-447.
- Scanlon, J.D. 1988. The snakes of Riversleigh. *Riversleigh Notes* 3: 7-8.
- Scanlon, J.D. (in press). Matsoiid snakes from the Eocene Tingamarra local fauna of eastern Queensland. *Kaupia: Darmstädter Beiträge zur Naturgeschichte* 2/3. Monument Grube Messel - Perspectives and Relationships.
- Simpson, G.G. 1933. A new fossil snake from the *Notostylops* beds of Patagonia. *Bulletin of the American Museum of Natural History* 67: 1-22.
- Smith, M.J. 1976. Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia. IV. Reptiles. *Transactions of the Royal Society of South Australia* 100 (1): 39-51.
- Smith, M.J. and Plane, M. 1985. Pythonine snakes (Boidae) from the Miocene of Australia. *Bureau of Mineral Resources Geology and Geophysics, Australia, Journal* 9: 191-195.
- Underwood, G. 1976. A systematic study of boid snakes. In: d'A. Bellairs, A. and Cox, C.B. (eds) *Morphology and Biology of Reptiles. Linnean Society Symposium Series 3*. Academic Press, London.
- Woodburne, M.O., Tedford, R.H., Archer, M., Turnbull, W.D., Plane, M.D. & Lundelius, E.L. 1985. Biochronology of the continental mammal record of Australia and New Guinea. *Special Publication, South Australian Department of Mines and Energy* 5: 347-363.

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#### NOTE ADDED IN PROOF

Since this paper was accepted for publication, eleven more matsoiid vertebrae from the Blast Site, Bullock Creek, have been examined, and all are considered to be derived from the *Y. camfieldensis* holotype skeleton. These newly prepared elements can be interpolated into the series of eighteen described in the text above, on the basis of both qualitative features of the various regions of the skeleton, and dimensions to be published later.

P908-4 is the axis, missing the anterior hypapophysis (which, as in most snakes, is sutured rather than fused to the centrum) and the left side of the neural arch. There is a good fit between the condyle of the axis and the cotyle of P895-5 (no. 1 in the series described above), showing that no. 1 is actually the third cervical vertebra, and the most anterior vertebra to bear ribs.

P895-28 and P895-22 are complete vertebrae bearing single hypapophyses, are very similar to each other in size and morphology, and come from the region between no. 4 and no. 5.

P908-1, P895-27, P895-25 and P895-23 are nearly complete vertebrae from between no. 10 and no. 11. All are larger than no. 11, but have the hypapophyses flat or double, and the zygosphenes somewhat concave above, so all must be posterior to no. 10. P908-1 is the largest vertebra yet known from this snake, with a width across the prezygapophyses of 46.4 mm.

P895-245, P908-2 and P895-24 are intermediate between no.13 and no.14. In P908-2 the zygapophyses, neural arch and zygosphenes are mostly broken away, but the other two speci-



mens are complete. P895-21 is a complete vertebra from between No. 16 and no.17.

Three significant segments of this skeleton remain unknown, namely the skull, the posterior trunk between no. 17 and no. 18, and the cloacal and caudal region. Hopefully the processing of more Blast Site material will produce the re-

quired specimens. The recovery of the additional Blast Site material listed here, also representing the holotype skeleton, and the absence of any other madtsoiid specimens from the Camfield Beds, confirms the interpretation of *Yurlunggur camfieldensis* as a rarely preserved element of the Bullock Creek Local Fauna.